

Mitigating the greenhouse gas balance of ruminant production systems through carbon sequestration in grasslands

J. F. Soussana^{1†}, T. Tallec¹ and V. Blanfort^{1,2}

¹INRA UR0874, UREP Grassland Ecosystem Research, 234, Avenue du Brézat, Clermont-Ferrand, F-63100, France; ²CIRAD UR 8, Livestock Systems, Campus International de Baillarguet, Cedex 5, Montpellier, F-34398, France

(Received 6 January 2009; Accepted 12 June 2009; First published online 22 September 2009)

Soil carbon sequestration (enhanced sinks) is the mechanism responsible for most of the greenhouse gas (GHG) mitigation potential in the agriculture sector. Carbon sequestration in grasslands can be determined directly by measuring changes in soil organic carbon (SOC) stocks and indirectly by measuring the net balance of C fluxes. A literature search shows that grassland C sequestration reaches on average $5 \pm 30 \text{ g C/m}^2$ per year according to inventories of SOC stocks and -231 and 77 g C/m^2 per year for drained organic and mineral soils, respectively, according to C flux balance. Off-site C sequestration occurs whenever more manure C is produced by than returned to a grassland plot. The sum of on- and off-site C sequestration reaches 129, 98 and 71 g C/m^2 per year for grazed, cut and mixed European grasslands on mineral soils, respectively, however with high uncertainty. A range of management practices reduce C losses and increase C sequestration: (i) avoiding soil tillage and the conversion of grasslands to arable use, (ii) moderately intensifying nutrient-poor permanent grasslands, (iii) using light grazing instead of heavy grazing, (iv) increasing the duration of grass leys; (v) converting grass leys to grass-legume mixtures or to permanent grasslands. With nine European sites, direct emissions of N_2O from soil and of CH_4 from enteric fermentation at grazing, expressed in CO_2 equivalents, compensated 10% and 34% of the on-site grassland C sequestration, respectively. Digestion inside the barn of the harvested herbage leads to further emissions of CH_4 and N_2O by the production systems, which were estimated at 130 g CO_2 equivalents/ m^2 per year. The net balance of on- and off-site C sequestration, CH_4 and N_2O emissions reached 38 g CO_2 equivalents/ m^2 per year, indicating a non-significant net sink activity. This net balance was, however, negative for intensively managed cut sites indicating a source to the atmosphere. In conclusion, this review confirms that grassland C sequestration has a strong potential to partly mitigate the GHG balance of ruminant production systems. However, as soil C sequestration is both reversible and vulnerable to disturbance, biodiversity loss and climate change, CH_4 and N_2O emissions from the livestock sector need to be reduced and current SOC stocks preserved.

Keywords: climate change, CO_2 , N_2O , CH_4 , soil organic carbon

Implications

The C sequestration potential by grasslands and rangelands could be used to partly mitigate the greenhouse gas (GHG) emissions of the livestock sector. This will require avoiding land use changes that reduce ecosystem soil C stocks (e.g. deforestation, ploughing up long-term grasslands) and a cautious management of pastures, aiming at preserving and restoring soils and their soil organic matter content. Combined with other mitigation measures, such as a reduction in the use of N fertilisers, of fossil-fuel energy and of N-rich feedstuffs by farms, this may lead to substantial reductions in GHG emissions per unit land area and per unit animal product.

Introduction

Grasslands cover about one-quarter of the earth's land surface (Ojima *et al.*, 1993) and span a range of climate conditions from arid to humid. Grasslands are the natural climax vegetation in areas (e.g. the Steppes of central Asia and the prairies of North America) where the rainfall is low enough to prevent the growth of forests. In other areas, where rainfall is normally higher, grasslands do not form the climax vegetation (e.g. north-western and central Europe) and are more productive. Rangelands are characterised by low-stature vegetation, owing to temperature and moisture restrictions, and found on every continent. Grasslands contribute to the livelihoods of over 800 million people, including many poor smallholders (Reynolds *et al.*, 2005)

[†] E-mail: soussana@clermont.inra.fr

and provide a variety of goods and services to support flora, fauna, and human populations worldwide. On a global scale, livestock use 3.4 billion hectares of grazing land (i.e. grasslands and rangelands), in addition to animal feed produced on about a quarter of the land under crops. By 2020, this agricultural sub-sector will produce about 30% of the value of global agricultural output (Delgado, 2005).

Agriculture accounted for an estimated emission of 5.1 to 6.1 Gigaton (Gt) CO₂ equivalents per year in 2005 (10% to 12% of total global anthropogenic emissions of greenhouse gases (GHGs) (Intergovernmental Panel on Climate Change (IPCC), 2007) and for ca. 60% of N₂O emissions and 50% of CH₄ emissions). Between 1990 and 2005, the direct emissions of the agriculture sector have increased by 17% and this increase has mostly occurred in developing countries (IPCC, 2007). The GHG inventory methodology used by IPCC (IPCC, 1996 and 2006) only includes, however, farm emissions in the agriculture sector. Indirect GHG emissions generated by farm activity through the use of farm inputs (e.g. fertilisers, feed, pesticides) do not belong to the agriculture sector, but are covered by other sectors such as industry (e.g. for the synthesis and packaging of inorganic N fertilisers and of organic pesticides) and transport (e.g. transport of fertilisers and feed). Emissions from electricity and fuel use are covered in the buildings and transport sector, respectively (IPCC, 2006).

Although the sectoral approach used by IPCC is appropriate for national and regional GHG inventories, it does not reflect emissions generated directly or indirectly by marketed products. Lifecycle analyses include indirect emissions generated by farm inputs and pre-chain activities. With this approach, it was estimated that livestock production systems, from feeding import to marketed animal products, generate directly and indirectly 18% of global GHG emissions as measured in CO₂ equivalents (Food and Agriculture Organisation (FAO), 2006). Livestock production induces 9% of global anthropogenic CO₂ emissions. The largest share (i.e. 7%) of this derives from land-use changes – especially deforestation – caused by expansion of pastures and arable land for feed crops. Livestock production systems also emit 37% of anthropogenic methane (see Martin *et al.*, 2009) most of that from enteric fermentation by ruminants. Furthermore, it induces 65% of anthropogenic nitrous oxide emissions, the great majority from manure (FAO, 2006).

Agricultural ecosystems hold large C reserves (IPCC, 2001), mostly in soil organic matter. Historically, these systems have lost more than 50 Gt C (Paustian *et al.*, 1998; Lal, 1999 and 2004). Agricultural lands generate very large CO₂ fluxes, both to and from the atmosphere (IPCC, 2001), but the *net* flux would be small (United States-Environmental Protection Agency (US-EPA), 2006). Nevertheless, soil C sequestration (enhanced sinks) is the mechanism responsible for most of the mitigation potential in the agriculture sector, with an estimated 89% contribution to the technical potential (IPCC, 2007), excluding, however,

the potential for fossil energy substitution through non-agricultural use of biomass. Worldwide the soil organic carbon (SOC) sequestration potential is estimated to be 0.01 to 0.3 Gt C/year on 3.7 billion ha of permanent pasture (Lal, 2004). Thus SOC sequestration by the world's permanent pastures could potentially offset up to 4% of the global GHG emissions.

Here, we review the C sequestration potential of temperate managed grasslands, focusing on Europe, and its role for mitigating the GHG balance of livestock production systems. We address the following issues: (i) carbon and GHG balance of managed grasslands, (ii) vulnerability of grassland C stocks to climate change and to biodiversity loss and (iii) the role of C sequestration for the GHG balance of ruminant production systems.

The carbon balance of managed grasslands

Organic carbon cycling in grasslands

The nature, frequency and intensity of disturbance play a key role in the C balance of grasslands. In a cutting regime, a large part of the primary production is exported from the plot as hay or silage, but part of these C exports may be compensated for by organic C imports through farm manure and slurry application.

Under intensive grazing, up to 60% of the above-ground dry-matter production is ingested by domestic herbivores (Lemaire and Chapman, 1996). However, this percentage can be much lower under extensive grazing. The largest part of the ingested C is digestible and, hence, is respired shortly after intake. The non-digestible C (25% to 40% of the intake according to the digestibility of the grazed herbage) is returned to the pasture in excreta (mainly as faeces). In most productive husbandry systems, the herbage digestibility tends to be maximised by agricultural practices such as frequent grazing and use of highly digestible forage cultivars. Consequently, in these systems the primary factor which modifies the C flux returned to the soil by excreta is the grazing pressure, which varies with the annual stocking rate (mean number of livestock units per unit area) (Sousana *et al.*, 2004). Secondary effects of grazing on the C cycle of a pasture include: (i) the role of excretal returns which, at a moderate rate of grazing intensity, could favour nutrient cycling and increase primary production, especially in nutrient-poor grasslands (De Mazancourt *et al.*, 1998); (ii) the role of defoliation intensity and frequency, and of treading by animals, which both reduce the leaf area and then the atmospheric CO₂ capture.

Only a small fraction of the ingested grassland C is accumulated by ruminants in meat production systems (e.g. 0.6% of C intake with heifers under continuous upland grazing; Allard *et al.*, 2007), but this fraction becomes much higher in intensive dairy production systems (e.g. 19% to 20% of C intake; Faverdin *et al.*, 2007). Additional C losses (ca. 3% to 5% of the digestible C) occur through methane emissions from the enteric fermentation (IPCC, 2006; see Martin *et al.*, 2009).

Processes controlling soil organic carbon accumulation

Carbon accumulation in grassland ecosystems occurs mostly below ground. Grassland soils are typically rich in SOC, partly owing to active rhizodeposition (Jones and Donnelly, 2004) and partly to the activity of earthworms that promote macro-aggregate formation in which micro-aggregates form that stabilise SOC for extended periods (Six *et al.*, 2002; Bossuyt *et al.*, 2005). Rhizodeposition favours C storage (Balesdent and Balabane, 1996), because direct incorporation into the soil matrix allows a high degree of physical stabilisation of the soil organic matter. Root litter transformation is also an important determinant of the C cycle in grassland ecosystems, which is affected both by the root litter quality and by the rhizosphere activity (Personeni and Loiseau, 2004 and 2005).

Below-ground C generally has slower turnover rates than above-ground C, as most of the organic C in soils (humic substances) is produced by the transformation of plant litter into more persistent organic compounds (Jones and Donnelly, 2004). Coarse soil organic matter fractions (above 0.2 mm) have a fast turnover in soils, and the mean residence time of C in these fractions is reduced by intensive compared to extensive management (Klump *et al.*, 2007). SOC may persist because it is bound to soil minerals and exists in forms that microbial decomposers cannot access (Baldock and Skjemstad, 2000). Therefore, SOC accumulation is often increased in clayey compared to sandy soils.

Sequestered SOC can, if undisturbed, remain in the soil for centuries. In native prairie sites in the US great plains, where SOC was ^{14}C -dated (Follett *et al.*, 2004), mean residence time of SOC in the soil increased but its concentration decreased with depth. Nevertheless, substantial amounts of SOC remained at depth even after several millennia. In an upland grassland in France, the mean residence time of SOC also increased with depth, reaching values of 2000 to 10 000 years in deep soil layer ($>0.2\text{ m}$) (Fontaine *et al.*, 2007). The lack of energy supply from fresh organic matter protects ancient buried organic C from microbial decomposition (Fontaine *et al.*, 2007). Therefore, agricultural practices like ploughing, which mix soil layers and break soil aggregates, accelerate SOC decomposition (Paustian *et al.*, 1998, Conant *et al.*, 2007).

While there has been a steady C accumulation in the soils of many ecosystems over millennia (Schlesinger, 1990), it is usually thought that soil C accumulation capacity is limited and that old non-disturbed soils should have reached after several centuries equilibrium in terms of their C balance (Lal, 2004). Soil C sequestration is reversible, as factors like soil disturbance, vegetation degradation, fire, erosion, nutrients shortage and water deficit may all lead to a rapid loss of SOC.

Role of land use change for carbon sequestration

Carbon sequestration can be determined directly by measuring changes in C pools (Conant *et al.*, 2001) and, or, indirectly by measuring C fluxes (Table 1 and equation (1)). SOC stocks display a high spatial variability (coefficient of

variation of 50%; Cannell *et al.*, 1999) in grassland as compared to arable land, which limits the accuracy of direct determinations of C stock changes. The variability in SOC contents is increased by sampling to different depths (Robles and Burke, 1998; Chevallier *et al.*, 2000; Bird *et al.*, 2002) and in pastures by excretal returns concentrated in patches.

Changes in SOC through time are non-linear after a change in land use or in grassland management. A simple two parameters exponential model has been used to estimate the magnitude of the soil C stock changes (Soussana *et al.*, 2004), showing that C is lost more rapidly than it is gained after a change in land use. Land use change from grassland to cropland systems causes losses of SOC in temperate regions ranging from 18% (± 4) in dry climates to 29% (± 4) in moist climates. Converting cropland back to grassland uses for 20 years was found to restore 18% (± 7) of the native C stocks in moist climates (relative to the 29% loss owing to long-term cultivation) and 7% (± 5) of native stocks in temperate dry climates (Conant *et al.*, 2001). As a result of periodic tillage and resowing, short-duration grasslands tend to have a potential for soil C storage intermediate between crops and permanent grassland. Part of the additional C stored in the soil during the grassland phase is released when the grassland is ploughed up. The mean C storage increases in line with prolonging the life-span of covers, that is, less frequent ploughing (Soussana *et al.*, 2004).

Role of management for carbon sequestration in grasslands

A number of studies have analysed effects of grassland and rangeland management on SOC stocks (Table 1). Most studies concern only the top-soil (e.g. 0 to 30 cm), although C sequestration or loss may also occur in deeper soil layers (Fontaine *et al.*, 2007). It is often assumed that impacts of management are greatest at the surface and decline with depth in the profile (Ogle *et al.*, 2004). A meta-analysis of 115 studies in pastures and other grazing lands worldwide (Conant *et al.*, 2001), indicated that soil C levels increased with improved management (primarily fertilisation, grazing management, and conversion from cultivation or native vegetation, improved grass species) in 74% of the studies considered (Table 1). Light grazing increased SOC stocks compared to enclosure and to heavy grazing (Ganjugunte *et al.*, 2005; Table 1). Some of the possible soil C sequestration opportunities for temperate grasslands in France have been calculated and compared (Table 1) for 20-year time periods (Soussana *et al.*, 2004). According to these estimates, annual C storage rates between 20 and 50 g C/m² per year are obtained for a range of options, which seem compatible with gradual changes in the forage production systems, namely: (i) reducing N fertiliser inputs in highly intensive grass leys; (ii) increasing the duration of grass leys; (iii) converting these leys to grass-legume mixtures or to permanent grasslands; (iv) moderately intensifying nutrient-poor permanent grasslands. By contrast, the intensification of nutrient-poor grasslands developed on organic soils may lead to large C losses, and the conversion

Table 1 Literature survey of net C storage (NCS) at grassland sites using different methods: C flux balance (A), grassland soil C inventory (B), soil C change after a change in grassland management (C), and farm scale flux measurements (D). A positive F_{CO_2} represents a net C uptake from the ecosystem. A positive NCS denotes a net carbon accumulation in grassland ecosystems. All fluxes are in g C/m² per year

Grassland type and management	Location	MAT (°C)	MAP (mm)	F_{CO_2} (g C/m ² per year)	$F_{harvest}$ (g C/m ² per year)	F_{manure} (g C/m ² per year)	NCS	Duration (months)	Method	References	Notes
A. Flux balance											
Alpine extensive pasture and hay meadow	Mount Rigi, Central Switzerland	8.4	991	−172	183	0	−355	12	Eddy covariance	Rogiers <i>et al.</i> (2008)	Drained organic soil
Grazed peat-pasture	Waikato, New Zealand	15	1281	−4.5	619	n.d.	−106	12	Eddy covariance	Nieveen <i>et al.</i> (2005)	Drained peat soil
Extensive grazed pasture	East of the Missouri river, North Dakota	15	483	317 _a	n.d.	n.d.	n.d.	10 × 6 months	Bowen Ratio	Phillips and Beeri (2008)	
Extensive grazed pasture	West of the Missouri river, North Dakota	15	390	239 _a	n.d.	n.d.	n.d.	10 × 6 months	Bowen ratio	Phillips and Beeri (2008)	
Extensive grazed pasture	Hungary	10.5	500	69	0	0	68	24	Eddy covariance	Soussana <i>et al.</i> (2007)	No N; dry steppe
Extensive grazed pasture	Italy	6.3	1200	360	0	0	358	24	Eddy covariance	Soussana <i>et al.</i> (2007)	90 kg N/ha per year
Intensive grassland (grazed and cut)	The Netherlands	10	780	177	220	80	33	12	Eddy covariance	Soussana <i>et al.</i> (2007)	300 kg N/ha per year
Intensive grassland (grazed and cut)	Scotland	8.8	638	343	110	3	231	24	Eddy covariance	Soussana <i>et al.</i> (2007)	200 kg N/ha per year
Intensive grassland (grazed and cut)	Ireland	9.4	824	293	374	0	−170	24	Eddy covariance	Soussana <i>et al.</i> (2007)	200 kg N/ha per year
Intensive meadow (cut)	Denmark	9.2	731	152	333	1400**	1100**	24	Eddy covariance	Soussana <i>et al.</i> (2007)	200 kg N/ha per year
Extensive pasture (grazed)	France	7	1200	75	0	0	69	36	Eddy covariance	Allard <i>et al.</i> (2007)	No fertilizer
Intensive pasture (grazed)	France	7	1200	99	0	0	87	36	Eddy covariance	Allard <i>et al.</i> (2007)	175 kg N/ha per year
Extensive meadow (cut)	Swiss	9.5	1100	254	311	0	−57	36	Eddy covariance	Ammann <i>et al.</i> (2007)	No fertilizer
Intensive meadow (cut)	Swiss	9.5	1100	467	368	67.5	147	36	Eddy covariance	Ammann <i>et al.</i> (2007)	200 kg N/ha per year
Intensive wetland meadow (grazed and cut)	UK	12.9	750	169	228	0	−34	12	Eddy covariance	Lloyd (2006)	Wet grassland; corrected for animal intake
Intensive grassland (Site A)	County Cork, southern Ireland	10	1470	15	0	n.d.	15**	12	Chamber measurements	Byrne <i>et al.</i> (2005)	300 kg N/ha per year. New pasture
Intensive grassland (Site B)	County Cork, southern Ireland	10	1470	38	0	n.d.	38**	12	Chamber measurements	Byrne <i>et al.</i> (2005)	300 kg N/ha per year. Permanent pasture
Native tallgrass prairie	North-central Oklahoma, USA	14	1868.5	8	0	0	n.d.	20	Eddy covariance	Suyker and Verma (2001)	Not grazed, prescribed burn
Sparse tussock dry grassland	South Island, New Zealand	9.9	446	−9	0	0	n.d.	24	Eddy covariance	Hunt <i>et al.</i> (2004)	Dry year, no N, no burning
Sparse tussock dry grassland	South Island, New Zealand	9.2	933	41	0	0	n.d.	24	Eddy covariance	Hunt <i>et al.</i> (2004)	Wet year, no N, no burning
Abandoned moist mixed grassland	Alberta, Canada	15.3	482	109	0	0	n.d.	12	Eddy covariance	Flanagan <i>et al.</i> (2002)	1998, wet summer
Abandoned moist mixed grassland	Alberta, Canada	13.2	341	21	0	0	n.d.	12	Eddy covariance	Flanagan <i>et al.</i> (2002)	1999, average summer
Abandoned moist mixed grassland	Alberta, Canada	14.5	275.5	−18	0	0	n.d.	12	Eddy covariance	Flanagan <i>et al.</i> (2002)	2000, dry summer
Mixed grass	Southeastern Arizona, USA	17	356	−135	0	0	n.d.	48	Bowen ratio	Emmerich (2003)	
Species-rich grassland	UK	n.d.	n.d.	n.d.	n.d.	n.d.	120	48	Chamber measurements	Fitter <i>et al.</i> (1997)	Four to five cuts per year

Table 1 Continued

Grassland type and management	Location	MAT (°C)	MAP (mm)	F _{CO₂}	F _{harvest} (g C/m ² per year)	F _{manure}	NCS	Duration (months)	Method	References	Notes
Grazed peat-pasture	California, USA	16.2	1180	28	0	0	n.d.	24	Eddy covariance	Xu and Baldocchi (2004)	
Mixed grass	Mandan ND, USA	n.d.	478	94	0	0	n.d.	4 × 7 months	Bowen ratio	Frank and Dugas (2001)	No fertilizer, no burning, last grazed: 4 years
B. Soil inventories											
Permanent grassland	England, Wales						−5	25 years	Soil C concentration change 0 to 15 cm	Bellamy <i>et al.</i> (2005)	
Upland grassland	England, Wales						−37.5	25 years	Soil C concentration change 0 to 15 cm	Bellamy <i>et al.</i> (2005)	
Rotational grass	England, Wales						−2.1	25 years	Soil C concentration change 0 to 15 cm	Bellamy <i>et al.</i> (2005)	
Grassland	Belgium						44	50 years	Soil C concentration change 0 to 30 cm	Goidts and van Wesemael, (2007)	
Grassland	Belgium						22	40 years	Soil C concentration change 0 to 30 cm	Lettens <i>et al.</i> (2005a)	
Grassland	Belgium						−90 (70)	10 years	Soil C concentration change 0 to 100 cm	Lettens <i>et al.</i> (2005b)	
Grassland	China						101	18 years	Soil C concentration change	Piao <i>et al.</i> (2009)	
C. Management change											
Perennial grassland converted from arable	Central Texas, USA						45	For 6 to 60 years	Soil C stock change 0 to 60 cm	Potter <i>et al.</i> (1999)	
Cultivated site to restored grassland	Missouri coteaux, Canada	0.7	320				30 to 290	8 years	Soil C stock change 0 to 30 cm	Nelson <i>et al.</i> (2008)	
Heavy to light grazing grassland	Cheyenne, WY, USA	n.d.	384				13.8	21 years	Soil C stock change 0 to 5 cm	Ganjugunte <i>et al.</i> (2005)	
Exclosure to light grazing	Cheyenne, WY, USA	n.d.	384				14.3	21 years	Soil C stock change 0 to 5 cm	Ganjugunte <i>et al.</i> (2005)	
Nutrients addition via fertilizer	Forty-two data points						30b		Soil C stock change	Conant <i>et al.</i> (2001)	
Converting cultivated land to grassland	Twenty-three data points						101b		Soil C stock change	Conant <i>et al.</i> (2001)	
Improved grazing management	Forty-five data points						35b		Soil C stock change	Conant <i>et al.</i> (2001)	
Improved grass species	Five data points						304b		Soil C stock change	Conant <i>et al.</i> (2001)	
Restoration of degraded lands	US great plains						80 to 110		Soil C stock change	Follett <i>et al.</i> (2001)	
Sown grassland on mineral soil	France						60 to 80		Soil C stock change (organic matter fractions >50 μ.)	Loiseau and Soussana (1999)	
Reduction of N fertilizer input	France	9	800				30	10 years	Soil C stock change 0 to 30 cm	Soussana <i>et al.</i> (2004)	

Table 1 Continued

Grassland type and management	Location	MAT (°C)	MAP (mm)	F _{CO₂}	F _{harvest} (g C/m ² per year)	F _{manure}	NCS	Duration (months)	Method	References	Notes
Conversion of short duration grass-ley to grass-legume	France	9	800				30 to 50	10 years	Soil C stock change 0 to 30 cm	Soussana <i>et al.</i> (2004)	
Intensification of permanent grassland	France	9	800				20	10 years	Soil C stock change 0 to 30 cm	Soussana <i>et al.</i> (2004)	
Intensification of nutrient poor grassland on organic soils	France	7	1100				−100	10 years	Soil C stock change 0 to 30 cm	Soussana <i>et al.</i> (2004)	
Permanent grassland to medium duration leys	France	9	800				−20	10 years	Soil C stock change 0 to 30 cm	Soussana <i>et al.</i> (2004)	
Increasing the duration of grass leys	France	9	800				20 to 50	10 years	Soil C stock change 0 to 30 cm	Soussana <i>et al.</i> (2004)	
Short duration leys to permanent grassland	France	9	800				30 to 40	10 years	Soil C stock change 0 to 30 cm	Soussana <i>et al.</i> (2004)	
D. Farm scale											
Intensive grazed and cut grassland	County Cork, southern Ireland	10	1340	290	134	n.d.	205	12	Eddy covariance, farm fluxes	Byrne <i>et al.</i> (2007)	300 kg N/ha per year; cattle grazed
Intensive grassland (grazed and cut)	South West Ireland	10	1785	193	70	n.d.	24	12	Eddy covariance, farm fluxes	Jaksic <i>et al.</i> (2006)	Wet year, 300 kg N/ha per year
Intensive grassland (grazed and cut)	South West Ireland	10	1185	258	100	n.d.	89	12	Eddy covariance, farm fluxes	Jaksic <i>et al.</i> (2006)	Dry year, 300 kg N/ha per year

MAT = mean annual temperature; MAP = mean annual precipitation; F_{CO₂} = net CO₂ ecosystem exchange; F_{manure} = lateral organic C fluxes which are imported (manure application) in the system; F_{harvest} = lateral organic C fluxes which are exported (harvests) from the system; n.d. = not defined.

a average of growing season.

b 87% of the studies were from Australia, the United Kingdom, New Zealand, Canada, Brazil and the United States.

**Not included in mean.

Additional studies can be found in the reviews by Conant *et al.* (2001) and by Ogle *et al.* (2004).

of permanent grasslands to leys of medium duration is also conducive to the release of soil C. Nevertheless, the uncertainties concerning the estimated values of C storage or release after a change in grassland management are still very high (estimated at 25 g C/m² per year).

Data from the National Soil Inventory of England and Wales obtained between 1978 and 2003 (Bellamy *et al.*, 2005) show that C was lost from most top soils across England and Wales over the survey period. Nevertheless, rotational grasslands gained C at a rate of ca. 10 g C/m² per year (Table 1). The Countryside Surveys of Great Britain are ongoing ecological assessments in UK that have taken place since 1978 (Firbank *et al.*, 2003). In this survey, significant increases in soil C concentration, ranging from 0.2 to 2.1 g/kg per year, were observed in both fertile and infertile grasslands (CLIMSOIL, 2008).

In Belgium, grasslands were reported either to be sequestering C in soils at rates of 22 or 44 g C/m² per year (Letten *et al.*, 2005a; Goidts and van Wesemael, 2007, respectively), or losing C at 90 g C/m² per year on podzolic, clayey and loam soils (Letten *et al.*, 2005b). However, soil bulk density was estimated from pedo-transfer functions in these studies, which adds to the uncertainty, as a small change in bulk density can result in a large change in stock of SOC (Smith *et al.*, 2007).

Follett and Schuman (2005) reviewed grazing land contributions to C sequestration worldwide using 19 regions. A positive relationship was found, on average, between the C sequestration rate and the animal stocking density, which is an indicator of the pasture primary productivity. Based on this relationship, they estimate a 200 Megatons SOC sequestration per year on 3.5 billion ha of permanent pasture worldwide. Using national grassland resource dataset and NDVI (Normalised Difference Vegetation Index) time series data, Piao *et al.* (2009) estimated that C stocks of China's grasslands increased over the past two decades by 117 and 101 g C/m² per year in the vegetation and soil compartments, respectively.

In their assessment of the European C balance, Janssens *et al.* (2003) concluded that grasslands were a highly uncertain component of the European-wide C balance in comparison to forests and croplands. They estimated a net grassland C sink of 66 ± 90 g C/m² per year over geographic Europe, though this estimate was not based on field data but on a simple model using yields and land-use data (Vleeshouwers and Verhagen, 2002).

The 2006 IPCC *Guidelines* allow for the estimation of: (i) C emissions and removals in grasslands owing to changes in stocks in above and below-ground biomass; (ii) emissions of non-CO₂ GHGs (CO, CH₄, N₂O and NO_x) owing to biomass burning (Fearnside, 2000); and (iii) C emissions and removals in grasslands owing to changes in soil C stocks. Mineral and organic soils (peat, histosols, etc.) are separated for the calculations of soil C stock changes, provided that national inventory data are available for grassland soils (IPCC, 2006). Ogle *et al.* (2004) identified 49 studies dealing with effects of management practices that either

degraded or improved conditions relative to nominally managed grasslands. On average, degradation reduced SOC stocks to 95% and 97% of C stored under nominal conditions in temperate and tropical regions, respectively. In contrast, improving grasslands with a single management activity enhanced SOC stocks by 14% and 17% in temperate and tropical regions, respectively, and with an additional improvement(s), stocks increased by another 11%. By applying these factors to managed grasslands in the USA, Ogle *et al.* (2004) found that over a 20-year period, changing management could sequester up to 142 Megatons C per year.

Estimating carbon sequestration from carbon flux measurements

An alternative to the direct measurement of C stock changes in grasslands is to measure the net balance of C fluxes (net C storage, NCS) exchanged at the system boundaries. This approach provides a high temporal resolution and changes in C stock can be detected within one year. In contrast, direct measurements of stock change require several years or several decades to detect significant effects, given the high variability among samples. The main drawback of flux measurements, however, is that several C fluxes need to be measured: (i) trace gases exchanged with the atmosphere (i.e. CO₂; CH₄; volatile organic compounds, VOC; and emissions during fires), (ii) organic C imports (manures) and exports (harvests, animal products), (iii) dissolved C lost in waters (dissolved organic and inorganic C) and lateral transport of soil C through erosion (Figure 1). NCS (g C/m² per year) is the

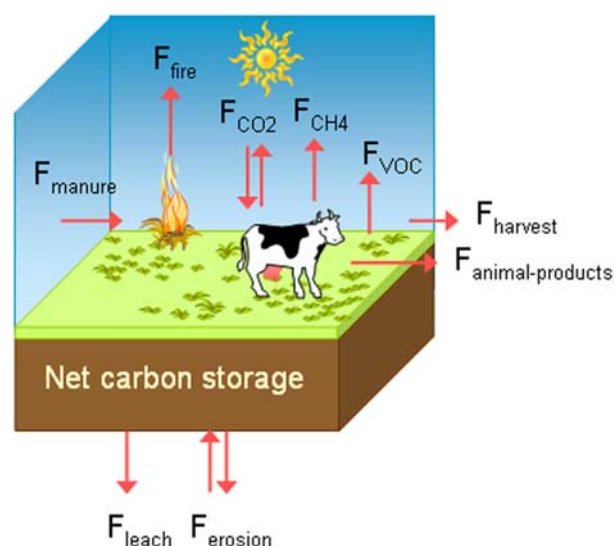


Figure 1 Carbon fluxes (g C/m² per year) in a managed grassland. F_{CO_2} is the net CO₂ ecosystem exchange. F_{fire} is the total C loss by fire; F_{CH_4} , F_{VOC} are non-CO₂ trace gas C losses from the ecosystem, as methane and volatile organic carbon, respectively. F_{manure} , $F_{harvest}$ and $F_{animal-products}$ are lateral organic C fluxes, which are either imported (manure application) or exported (harvests and animal products) from the system. F_{leach} and $F_{erosion}$ are organic (and/or inorganic) C losses through leaching and erosion, respectively. Net carbon storage (NCS, see equation (1)) is calculated as the balance of carbon fluxes.

mass balance of these fluxes (equation (1)):

$$\text{NCS} = (\text{F}_{\text{CO}_2} - \text{F}_{\text{CH}_4-\text{C}} - \text{F}_{\text{VOC}} - \text{F}_{\text{fire}}) + (\text{F}_{\text{manure}} - \text{F}_{\text{harvest}} - \text{F}_{\text{animal-products}}) - (\text{F}_{\text{leach}} + \text{F}_{\text{erosion}}), \quad (1)$$

where F_{CO_2} is equal to the net ecosystem exchange (NEE) of CO_2 between the ecosystem and the atmosphere, which is conventionally positive for a C gain by the ecosystem. $\text{F}_{\text{CH}_4-\text{C}}$, F_{VOC} and F_{fire} are trace gas C losses from the ecosystem (g C/m^2 per year). F_{manure} , $\text{F}_{\text{harvest}}$ and $\text{F}_{\text{animal-products}}$ are lateral organic C fluxes (g C/m^2 per year), which are either imported or exported from the system. F_{leach} and $\text{F}_{\text{erosion}}$ are organic (and/or inorganic C losses in g C/m^2 per year) through leaching and erosion, respectively.

Nevertheless, depending on the system studied and its management, some of these fluxes can be neglected for NCS calculation. For instance, fire emissions by grasslands are very low in temperate regions like Europe (i.e. below 1 g C/m^2 per year over 1997 to 2004), while they reach 10 and 100 g C/m^2 per year in the Mediterranean and in tropical grasslands, respectively (Van der Werf *et al.*, 2006). Erosion ($\text{F}_{\text{erosion}}$) is also rather insignificant in permanent grasslands (e.g. in Europe), but can be increased by tillage in the case of sown grasslands. The global map of $\text{F}_{\text{erosion}}$ created by Van Oost *et al.* (2007) indicates that grassland C erosion rates are usually below 5 g C/m^2 per year, even in tropical dry grasslands (Van Oost *et al.*, 2007). The total dissolved C loss by leaching was estimated by Siemens (2003) and Janssens *et al.* (2003) at $11 \pm 8 \text{ g C/m}^2$ per year for Europe. This flux tends to be highly variable depending on soil (pH, carbonate) and climate (rainfall, temperature) factors, and it could reach higher values in wet tropical grasslands, especially on calcareous substrate. VOC emissions by grassland systems are increased in the short-term by cutting and tend to be higher with legumes than with grass species (Davison *et al.*, 2008). However, these C fluxes are usually small and can easily be neglected. Therefore, with temperate managed grasslands, equation (1) can be simplified as (Allard *et al.*, 2007):

$$\text{NCS} = (\text{F}_{\text{CO}_2} - \text{F}_{\text{CH}_4-\text{C}}) + (\text{F}_{\text{manure}} - \text{F}_{\text{harvest}} - \text{F}_{\text{animal-products}}) - \text{F}_{\text{leach}}. \quad (2)$$

With the advancement of micrometeorological studies of the ecosystem-scale (F_{CO_2}) exchange of CO_2 (Baldocchi and Meyers, 1998), eddy flux covariance measurement techniques have been applied to grassland and rangelands. As the measurement uses a free-air technique, as opposed to enclosures, there is no disturbance of the measured area that can be freely accessed by herbivores. Ruminant's belched CO_2 (digestive + metabolic CO_2) at grazing, which can be measured by the SF_6 method (Pinares-Patino *et al.*, 2007), is included in F_{CO_2} measurements. It has no direct effect on the atmospheric CO_2 concentration, because it is 'short-cycling' carbon, which has been fixed by plants earlier.

Gilmanov *et al.* (2007) have analysed tower CO_2 flux measurements from 20 European grasslands, covering a

wide range of environmental and management conditions. F_{CO_2} varies from significant net uptake (650 g C/m^2 per year) to significant release (160 g C/m^2 per year). Four sites became CO_2 sources in some years, two of them during drought events and two of them with a significant peat horizon (Gilmanov *et al.*, 2007). Therefore, net CO_2 release ($\text{F}_{\text{CO}_2} < 0$) is associated with organic-rich soils and heat stress. Indeed, a net CO_2 release was found with drained organic soils subjected to grazing in Switzerland and in New Zealand (Nieveen *et al.*, 2005; Rogiers *et al.*, 2008), and these sites were found to lose C (i.e. negative NCS; Table 1).

Within the European (FP5 EESD) 'GreenGrass' project, the full GHG balance of nine contrasted grassland sites covering a major climatic gradient over Europe (Tables 1 and 2), was measured during two complete years (Soussana *et al.*, 2007). The sites include a wide range of management regimes (rotational grazing, continuous grazing and mowing), the three main types of managed grasslands across Europe (sown, intensive permanent and semi-natural grassland) and contrasted nitrogen fertiliser supplies. Two sites (in Ireland and in Switzerland; Table 1) were sown grass-legume mixtures, while the remainder were long-term grasslands. At all sites, the NEE of CO_2 was assessed using the eddy covariance technique. CH_4 emissions resulting from enteric fermentation of the grazing cattle were measured *in situ* at four sites using the SF_6 tracer method. N_2O emissions were monitored using various techniques (GC-cuvette systems, automated chambers and tunable diode laser).

The average C storage was initially estimated at $104 \pm 73 \text{ g C/m}^2$ per year, but without accounting for C leaching and for C exports in animal products (Soussana *et al.*, 2007). NCS and component fluxes are shown in Figure 2. Results, corrected for animal exports ($\text{F}_{\text{animal-products}}$) and for C leaching (F_{leach}), show that NCS varied between 50 and 129 g C/m^2 per year and was higher in grazed than in cut grasslands (Figure 2). Across sites, NCS declined with the degree of herbage utilisation by herbivores through grazing and cutting (Soussana *et al.*, 2007), which underlines that grassland C sequestration per unit area is favoured by extensive management provided that nutrients are not limiting (Allard *et al.*, 2007; Klumpp *et al.*, 2007). The uncertainty associated to NCS can be estimated using Gaussian error propagation rules and accounting for site number in each management type. NCS uncertainty reached 25% and 80% of the mean (data not shown) for grazed and for cut and mixed systems, respectively. Indeed, Ammann *et al.* (2007) reported that cutting and manure application introduce further uncertainties in NCS estimates.

A literature search shows that grassland C sequestration reaches on average $5 \pm 30 \text{ g C/m}^2$ per year according to inventories of SOC stocks and $22 \pm 56 \text{ g C/m}^2$ per year according to C flux balance (Table 1). These two estimates are therefore not significantly different, although there has not yet been any direct comparison at the same site between C flux and C stock change measurements. According to both flux (-231 and 77 g C/m^2 per year, respectively, Table 1A) and inventory (Bellamy *et al.*, 2005)

Table 2 Mean annual greenhouse fluxes in CO₂ equivalents/m² per year of managed European grassland sites studied by Soussana et al. (2007)

Management	NCS	Att-NCS	Grassland methane GWP _{CH₄} F _{CH₄}	Total methane GWP _{CH₄} F _{CH₄}	Grassland N ₂ O GWP _{N₂O} F _{N₂O}	Total N ₂ O GWP _{N₂O} F _{N₂O}	NGHG	Att-NGHG
Grazing	471	471	145	145	22	22	320	320
Grazing and cutting	183	268	159	476	64	81	-22	-272
Cutting	259	359	0	447	30	53	230	-141

NCS = net carbon storage in the grassland (see equation (2)); Att-NCS = attributed net carbon storage (see equation (4)); NGHG = net greenhouse gas balance (see equation (3)); Att-NGHG = attributed net greenhouse gas balance (see equation (5)); GWP = global warming potential.

Data are means of two, four and three European sites for grazed only (meat production systems), cut and grazed (meat and dairy production systems), and cut only (dairy production systems) grasslands.

A positive value of NCS, Att-NCS, NGHG and Att-NGHG denotes a sink activity of the grassland ecosystems.

methods, organic soils would be more susceptible of losing carbon than mineral soils, which underlines the need to preserve high soil C stocks.

Carbon flux studies show that NCS is affected by a number of site-specific factors, including grassland type (newly established *v.* permanent, Byrne *et al.*, 2005), N fertiliser supply (Ammann *et al.*, 2007), grazing pressure (Allard *et al.*, 2007), drainage (Nieveen *et al.*, 2005; Rogiers *et al.*, 2008) and burning (Suyker and Verma, 2001) (Table 1). In addition, annual rainfall, temperature and radiation (Hunt *et al.*, 2004; Ciais *et al.*, 2005; Gilmanov *et al.*, 2007; Soussana *et al.*, 2007) play an important role for the variability in NCS between years and between sites. Other possibly overlooked factors in C flux studies include past changes in land use (e.g. from arable to grassland) and grassland management (e.g. increased fertilisation, reduced herbage utilisation by grazing and cutting), which have carry-over effects on soil C pools. In addition, the recent rise in air temperature, in atmospheric CO₂ concentration and in N deposition has enhanced plant growth in northern mid-latitudes and high latitudes (Nemani *et al.*, 2003). Global change would therefore force grassland soils out of equilibrium, possibly leading to a transient increase in SOC stocks in temperate regions as a result of increased net primary productivity. Further research is needed to disentangle such global factors from management factors, in order to attribute grassland C sequestration to direct anthropogenic changes (land use and land management) and/or to climatic and atmospheric changes.

The greenhouse gas balance of managed grasslands

When assessing the impact of land use and land-use change on GHG emissions, it is important to consider the impacts on all GHGs (Robertson *et al.*, 2000). N₂O and CH₄ emissions are often expressed in terms of CO₂ equivalents, which is possible because the radiative forcing of nitrous oxide, methane and carbon dioxide, can be integrated over different timescales and compared to that for CO₂. For example, over the 100-year timescale, on a kilogram-for-kilogram basis, one unit of nitrous oxide has the same global warming potential (GWP) as 298 units of carbon dioxide (GWP_{N₂O} = 298), whereas one unit of methane has

the same GWP as 25 units of carbon dioxide (GWP_{CH₄} = 25) (IPCC, 2007). An integrated approach is needed to quantify in CO₂ equivalents the fluxes of all the three trace gases (CO₂, CH₄ and N₂O).

Management choices to reduce emissions involve important trade-offs: for example, preserving grasslands and adapting their management to improve C sequestration in the soil may actually increase N₂O and CH₄ emissions at farm scale. As agricultural management is one of the key drivers of the sequestration and emission processes, for grasslands there is potential to reduce the net GHG flux, expressed in CO₂ equivalents. Methane emissions by enteric fermentation under grazing conditions are reviewed in details by Martin *et al.* (2009). Below, we focus on N₂O emissions and on the GHG balance in CO₂ equivalents.

Nitrous oxide emissions from grassland soils

Biogenic emissions of N₂O from soils result primarily from the microbial processes nitrification and denitrification. N₂O is a by-product of nitrification and an intermediate during denitrification. Nitrification is the aerobic microbial oxidation of ammonium to nitrate and denitrification is the anaerobic microbial reduction of nitrate through nitrite, nitric oxide (NO) and N₂O to N₂. Nitrous oxide is a gaseous product that may be released from both processes to the soil atmosphere.

Major environmental regulators of these processes are temperature, pH, soil moisture (i.e. oxygen availability) and C availability (Velthof and Oenema, 1997). In most agricultural soils, biogenic formation of N₂O is enhanced by an increase in available mineral nitrogen, which in turn increases nitrification and denitrification rates. Hence, in general, addition of fertiliser N or manures and wastes containing inorganic or readily mineralisable N, will stimulate N₂O emission, as modified by soil conditions at the time of application. N₂O losses under anaerobic conditions are usually considered more important than nitrification-N₂O losses under aerobic conditions (Skiba and Smith, 2000).

For given soil and climate conditions, N₂O emissions are likely to scale with the nitrogen fertiliser inputs. Therefore, the current IPCC (2006) methodology assumes a default emission factor (EF₁) of 1% (ranging from 0.3% to 3%) for non-tropical soils emitted as N₂O per unit nitrogen input N (0.003 to 0.03 kg N₂O-N/kg N input).

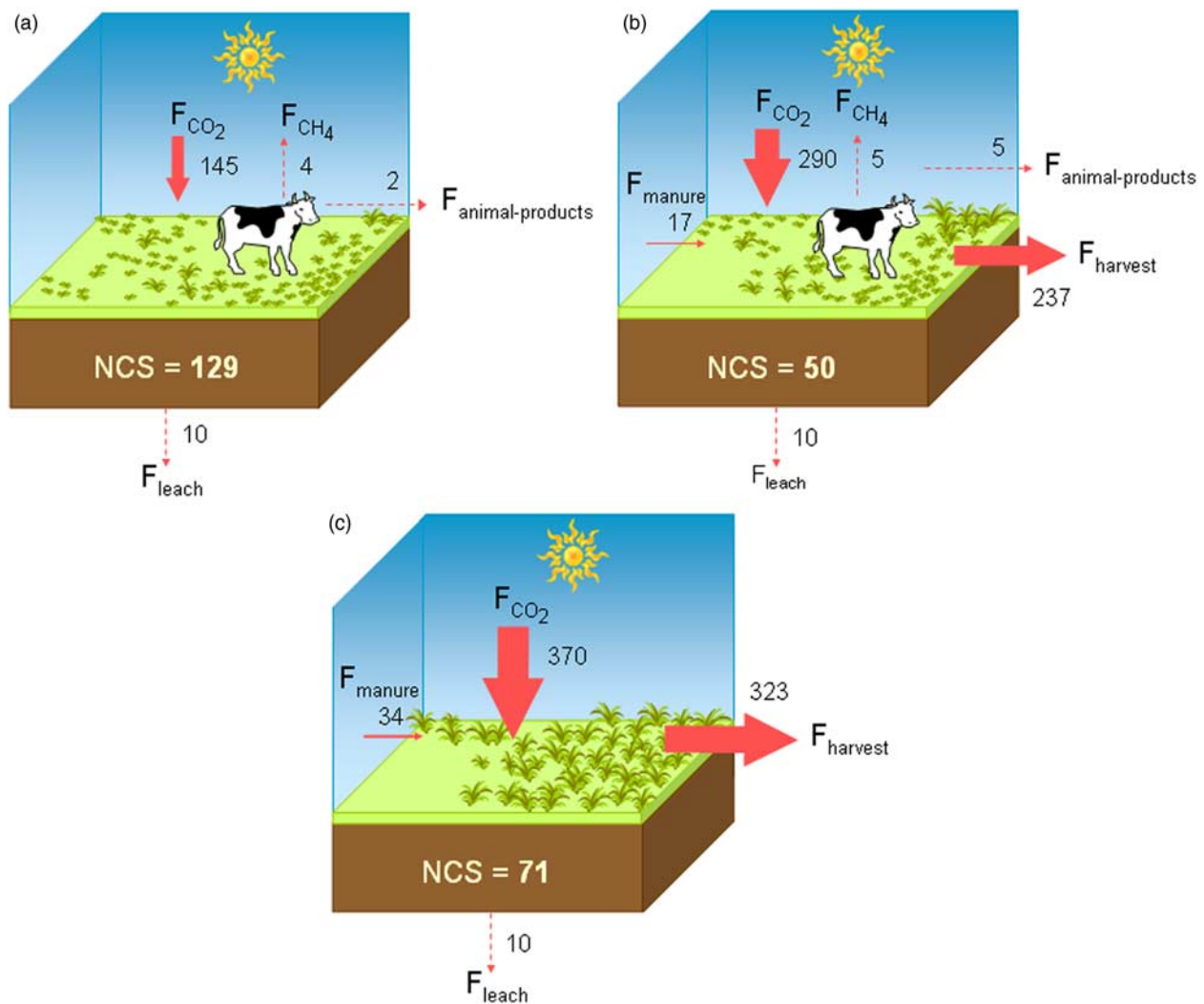


Figure 2 Carbon fluxes (g C/m^2 per year) in managed European grassland systems studied by Soussana *et al.* (2007). Net carbon storage in the grassland (NCS, see equation (2)) in (a) grazed only, (b) cut and grazed and (c) cut only grasslands is calculated as the balance of carbon fluxes. For abbreviations, see Figure 1. Data are means of two, four and three European sites for grazed only ((a), meat production systems), cut and grazed ((b), meat and dairy production systems) and cut only ((a), dairy production systems) grasslands. A standard F_{leach} value (10 g C/m^2 per year) was assumed for all sites. C exports in animal products were assumed to reach 2% and 20% of C intake for meat and milk production, respectively (see text). Grazed sites: Hungary, France, Italy (see Allard *et al.*, 2007; Soussana *et al.*, 2007; Table 1). Cut and grazed sites: Scotland, Ireland and the Netherlands (see Soussana *et al.*, 2007; Table 1). Cut sites: Switzerland (see Ammann *et al.*, 2007; Table 1). A positive value of NCS and attributed NCS denotes a sink activity of the grassland ecosystem.

N_2O emissions in soils usually occur in 'hot spots' associated with urine spots and particles of residues and fertiliser, despite the diffused spreading of fertilisers and manure (Flechar *et al.*, 2007). Nitrous oxide emissions from grasslands also tend to occur in short-lived bursts following the application of fertilisers (Clayton *et al.*, 1997; Leahy *et al.*, 2004). Temporal and spatial variations contribute large sources of uncertainty in N_2O fluxes at the field and annual scales (Flechar *et al.*, 2005). The overall uncertainty in annual flux estimates derived from chamber measurements may be as high as 50% owing to the temporal and spatial variability in fluxes, which warrants the future use of continuous measurements, if possible at the field scale (Flechar *et al.*, 2007). In the same study, annual emission factors for fertilised systems were highly variable, but the mean emission factor (0.75%) was substantially lower than the IPCC

default value of 1.0% for direct emissions of N_2O from N fertilisers (Flechar *et al.*, 2007).

The relationship, on a global basis, between the amount of N fixed by chemical, biological or atmospheric processes entering the terrestrial biosphere, and the total emission of N_2O shows an overall conversion factor of 3% to 5% (Crutzen *et al.*, 2007). This factor is covered only in part by the 1% of direct emissions factor. Additional indirect emissions, resulting from further N_2O emissions at the landscape scale, are also accounted for by IPCC (2006).

Methane exchanged with grassland soils

In soils, methane is formed under anaerobic conditions at the end of the reduction chain when all other electron acceptors such as, for example, nitrate and sulphate, have been used. Methane emissions from freely drained grassland

soils are, therefore, negligible. In fact, aerobic grassland soils tend to oxidise methane at a larger rate than cropland soil (6 and 3 kg CH₄/ha per year respectively), but less so than uncultivated soils (Boeckx and Van Cleemput, 2001). In contrast, in wet grasslands as in wetlands, the development of anaerobic conditions in soils may lead to methane emissions. In an abandoned peat meadow, methane emissions were lower in water-unsaturated compared to water-saturated soil conditions (Hendriks *et al.*, 2007). Keppler *et al.* (2006) have shown the emissions of low amounts of CH₄ by terrestrial plants under aerobic conditions. However, this claim has not been confirmed since and was shown to be caused by an experimental artefact (Dueck *et al.*, 2007).

Budgeting the greenhouse gas balance of grasslands

Budgeting equations can be extended to include fluxes ($F_{\text{CH}_4-\text{C}}$ and $F_{\text{N}_2\text{O}}$) of non-CO₂ radiatively active trace gases and calculate a net exchange rate in CO₂ equivalents (net greenhouse gas balance, NGHG; g CO₂/m² per year, equation (3)), using the GWP of each gas at the 100-years time horizon (IPCC, 2007):

$$\text{NGHG} = k_{\text{CO}_2}(\text{NCS} + F_{\text{CH}_4-\text{C}}) - \text{GWP}_{\text{CH}_4}F_{\text{CH}_4} - \text{GWP}_{\text{N}_2\text{O}}F_{\text{N}_2\text{O}}, \quad (3)$$

where $k_{\text{CO}_2} = 44/12$ g CO₂-g C, F_{CH_4} is the methane emission (g CH₄/m² per year) and $F_{\text{N}_2\text{O}}$ is the nitrous oxide emission (g N₂O/m² per year). CH₄ is not double counted as CO₂ in equation (4), as $F_{\text{CH}_4-\text{C}}$ is added to NCS.

On average, of the nine sites covered by the 'GreenGrass' European project, the grassland plots displayed annual N₂O and CH₄ emissions of 39 and 101 g CO₂ equivalents/m² per year, respectively (Table 2). Hence, when expressed in CO₂ equivalents, emissions of N₂O and CH₄ compensated 10% and 34% of the on-site grassland C sequestration, respectively. The mean on-site NGHG reached 198 g CO₂ equivalents/m² per year, indicating a sink for the atmosphere. Nevertheless, sites that were intensively managed by grazing and cutting had a negative NGHG and were therefore estimated to be GHG sources in CO₂ equivalents.

Vulnerability of soil organic carbon to climate change

Although the ancient carbon located in the deep soil is presumably protected from microbial decomposition by a lack of easily degradable substrates (Fontaine *et al.*, 2003), soil C stocks in grassland ecosystems are vulnerable to climate change. The 2003 heat wave and drought reduced by 30% the total gross primary productivity over Europe, which resulted in a strong anomalous net source of carbon dioxide (0.5 Gt C per year) to the atmosphere and reversed the effect of 4 years of net ecosystem C sequestration (Ciais *et al.*, 2005). An increase in future drought events could therefore turn temperate grasslands into C sources, contributing to positive carbon-climate feedbacks already anticipated in the tropics and at high latitudes (Betts *et al.*, 2004; Ciais *et al.*, 2005; Bony *et al.*, 2006). Gilmanov *et al.* (2005) have also shown that a source

type of activity is not an exception for the mixed prairie ecosystems in North America, especially during years with lower than normal precipitation.

The atmospheric conditions that result in such heat-wave conditions are likely to increase in frequency (Meehl and Tebaldi, 2004) and may approach the norm by 2080 under scenarios with high GHG emissions (Beniston, 2004; Schär and Jendritzky, 2004). The rise in atmospheric CO₂ reduces the sensitivity of grassland ecosystems to drought (Morgan *et al.*, 2004) and increases grassland productivity by 5% to 15% depending on water and nutrients availability (Soussana and Hartwig, 1996; Soussana *et al.*, 1996; Tubiello *et al.*, 2007). However, these positive effects are unlikely to offset the negative impacts of high temperature changes and reduced summer rainfall, which would lead to more frequent and more intense droughts (Lehner *et al.*, 2006) and, presumably, C loss from soils.

The possible implication of climate change was studied by Smith *et al.* (2005) who calculated soil C change using the Rothamsted carbon model and using climate data from four global climate models implementing four IPCC emission scenarios. Changes in net primary production (NPP) were calculated by the Lund-Potsdam-Jena model. Land-use change scenarios were used to project changes in cropland and grassland areas. Projections for 1990 to 2080 for mineral soil show that climate effects (soil temperature and moisture) will tend to speed decomposition and cause soil C stocks to decrease, whereas increases in C input because of increasing NPP could slow the loss.

According to empirical niche-based models, projected changes in temperature and precipitation are likely to lead to large shifts in the distribution of plant species, with negative effects on biodiversity at regional and global scales (Thomas *et al.*, 2004; Thuiller *et al.*, 2005). Although such model predictions are highly uncertain, experiments do support the concept of fast changes in plant species composition and diversity under elevated CO₂, with complex interactions with warming and changes in rainfall (Teyssonneyre *et al.*, 2002; Picon-Cochard *et al.*, 2004). Indeed, warming and altered precipitation have been shown to affect plant community structure and species diversity in rainfall manipulation experiments (Zavaleta *et al.*, 2003; Klein *et al.*, 2005).

Biodiversity experiments have shown causal relationships between species number or functional diversity, ecosystem productivity (e.g. Tilman *et al.*, 1997; Hector *et al.*, 1999; Röscher *et al.*, 2005) and C sequestration (Tilman *et al.*, 2006a and 2006b, Klumpp and Soussana, 2009). Therefore, another threat to C sequestration by grassland soils stems from the rapid loss of plant diversity, which is projected under climate change.

The role of grassland carbon sequestration for the GHG balance of livestock systems

There are still substantial uncertainties in most components of the GHG balance of livestock production systems. Methods developed for national and global GHG inventories

are inaccurate at the farm scale. Livestock production systems can be ranked differently depending on the approach (plot scale, on farm budget, lifecycle analysis) and on the criteria (emissions per unit land area or per unit animal product) selected (Schils *et al.*, 2007). Moreover, C sequestration (or loss) plays an important (Table 1D), but often neglected, role in the farm GHG budget.

Carbon transfer between different fields is very common in livestock production systems. The application of organic manure to certain fields may also strongly vary from year to year (depending for example on the nutrient status). To date, grassland C sequestration has mostly been studied at the field scale, neglecting the post-harvest fate of the cut herbage. The calculation of NCS considers that the total carbon in the harvested herbage returns within one year to the atmosphere. This is usually not the case, as the non-digestible carbon in this pool will be excreted by ruminants and incorporated into manure that will be spread after storage either on the same or on another field. Off-site C sequestration will occur whenever more C manure is produced by than that returned to a grassland plot. To make some progress, we estimate below the off-site C and GHG balance of the harvested herbage.

Carbon balance during housing

When considering an off-site balance, the system boundaries need to be defined. In the barn, ruminant's digestion of the harvested herbage (F_{harvest}) leads to additional C losses as respiratory CO_2 and methane from enteric fermentation and to the production of animal effluents (manure). The manure generated by harvests from a given grassland field will be brought to other fields (grassland or arable) thereby contributing to their own carbon budgets. To avoid double counting, we only attribute to a given grassland field the surplus, if any, of decomposed C manure that it generates compared to the amount of manure it receives (Figure 3). On-site decomposition of manure C supplied to the studied grassland field contributes to ecosystem respiration (F_{CO_2} ; equation (2)) and is therefore not double counted as an off-site CO_2 flux.

Off-site C sequestration ($\text{NCS}_{\text{@barn}}$) is calculated as the SOC derived from cut herbage manure that is not returned to the grassland, taking into account CH_4 emission from manure management. By adding off-site C sequestration and on-site C sequestration (NCS), an attributed NCS (Att-NCS) is calculated as:

$$\begin{aligned} \text{Att-NCS} &= \text{NCS} + \text{NCS}_{\text{@barn}} = \text{NCS} \\ &+ f_{\text{humif}} \cdot \text{Max}[0, (1 - f_{\text{digest}})F_{\text{harvest}} - F_{\text{manure}}] \\ &- F_{\text{CH}_4\text{manure_C}}, \end{aligned} \quad (4)$$

where f_{humif} is the fraction of non-labile C in manure, f_{digest} is the proportion of ingested C that is digestible and $F_{\text{CH}_4\text{manure_C}}$ is methane emission from farm effluents calculated according to IPCC (2006) Tier 2 method in CO_2 -C equivalents (Figure 3). The fraction of non-labile C in manure (f_{humif}) varies between 0.25 and 0.45 (Soussana *et al.*, 2004).

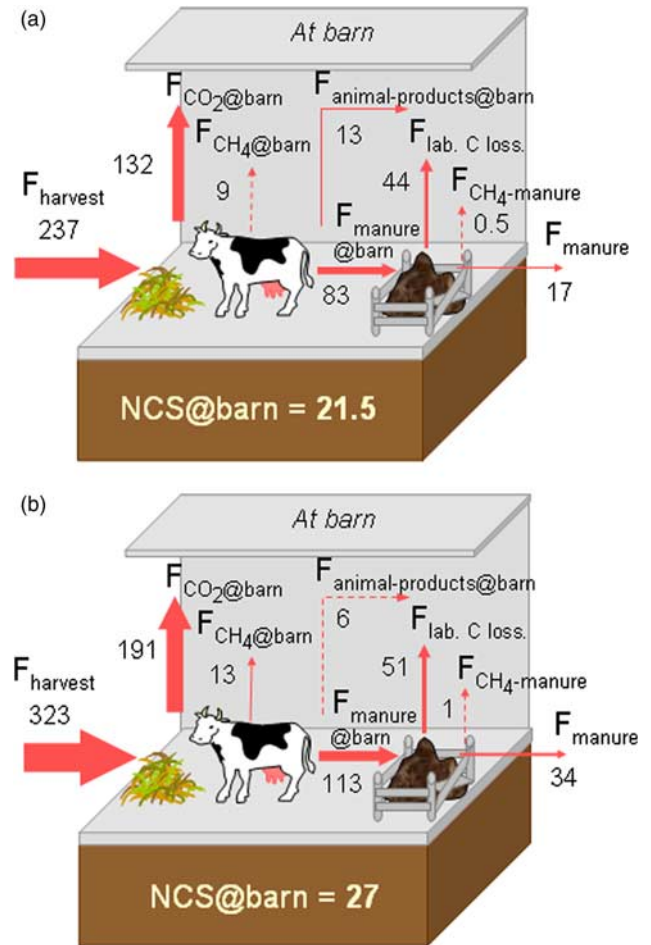


Figure 3 Carbon fluxes (g C/m^2 per year) in managed European grassland systems studied by Soussana *et al.* (2007). Net carbon storage in the barn ($\text{NCS}_{\text{@barn}}$) in (a) cut and grazed and (b) cut only grasslands are calculated as the balance of carbon fluxes. $F_{\text{CO}_2\text{@barn}}$, $F_{\text{animal-products@barn}}$ and $F_{\text{labile-C-losses}}$ are, respectively, CO_2 emissions, C exports in animal products from ruminants and CO_2 losses from microbial degradation of farm effluents during storage and after spreading. $F_{\text{CH}_4\text{@barn}}$ and $F_{\text{CH}_4\text{-manure}}$ are the CH_4 emissions at barn from enteric fermentation and farm effluents, respectively. For other abbreviations, see Figure 1. Carbon fluxes at barn were estimated assuming the same type of production (meat or milk) in the barn and in the grassland and solid manure (see equation (4)). C exports in animal products at barn were assumed to be 2% and 20% of C intake for meat and milk production, respectively (see text).

Equation (3) assumes that (i) all harvested C is ingested by ruminants (no post-harvest losses), and (ii) that the non-digestible fraction returned as excreta is used for spreading. These assumptions could lead to an overestimation of the attributed NCS, as additional C losses take place after forage harvests (during hay drying and silage fermentation) as well as in manure storage systems. However, these losses concern the degradable fraction of manures and are thus already accounted for by the f_{humif} coefficient.

$\text{NCS}_{\text{@barn}}$ reached 21.5 and 27 g C/m^2 per year for mixed and cut systems, respectively. Therefore, Att-NCS, which includes $\text{NCS}_{\text{@barn}}$, was higher in grazed (129 g C/m^2 per year) than in cut and mixed grassland systems (98.5 and 71 g C/m^2 per year, respectively). These estimates do not

include C emissions from machinery, which are higher in cut (e.g. mowing, silage making) compared to grazed systems, but are not part of the AFOLU (Agriculture, Forestry and Other Land Uses) sector and are not discussed in this review.

GHG balance during housing

GHG emissions from manure management include direct emissions of CH₄ and N₂O, as well as indirect emissions of N₂O derived from NH₃/NO_x. Quantification of GHG emissions from manure are typically based on national statistics for manure production and housing systems combined with emission factors which have been defined by the IPCC or nationally (Petersen *et al.*, 2002). The quality of GHG inventories for manure management is critically dependent on the applicability of these emission factors.

Animal manure is collected as solid manure and urine, as liquid manure (slurry) or as deep litter, or it is deposited outside in drylots or on pastures. These manure categories represent very different potentials for GHG emissions, as also reflected in the methane conversion factors and nitrous oxide emission factors, respectively. However, even within each category the variations in manure composition and storage conditions can lead to highly variable emissions in practice. This variability is a major source of error in the quantification of the GHG balance for a system. To the extent that such variability is influenced by management and/or local climatic conditions, it may be possible to improve the procedures for estimating CH₄ and N₂O emissions from manure (Sommer *et al.*, 2004).

The fraction of non-labile C (f_{humif}) in manure increases from 0.25 to about 0.5 after composting (Rémy and Marin-La Flèche, 1976). During composting, the more degradable organic compounds are decomposed and the residual compounds, which tend to have a longer life span, increase in concentration. In one study, cumulative C losses during storage and after incubation in the soil accounted for 60% and 54% of C initially present in composted and anaerobically stored manure, respectively (Thomsen and Olesen, 2000).

In order to account for: (i) the offsite CO₂, CH₄ and N₂O emissions resulting directly from the digestion by cattle of the forage harvests, (ii) the contribution to CH₄ and N₂O emissions by farm effluents and (iii) the manure and slurry applications which add organic C to the soil, an attributed net GHG balance (Att-NGHG) was adapted from Soussana *et al.* (2007) as:

$$\begin{aligned} \text{Att-NGHG} = & k_{CO_2}(\text{Att-NCS} + F_{CH_4-C}) - GWP_{CH_4}(F_{CH_4} \\ & + F_{CH_4@barn} + F_{CH_4-manure}) - GWP_{N_2O}(F_{N_2O} \\ & + F_{N_2O-manure}), \end{aligned} \quad (5)$$

where $F_{CH_4@barn}$ is CH₄ emission by enteric fermentation at barn (g CH₄/m² per year), $F_{CH_4-manure}$ (g CH₄/m² per year) and $F_{N_2O-manure}$ (g N₂O/m² per year) are the CH₄ and direct N₂O emissions from farm effluents, respectively, which were calculated according to IPCC (2006) Tier 2 method (Table 2).

Estimated methane emissions at barn from cut herbage reached up to 447 g CO₂ equivalents/m² per year (Table 2) and were therefore an important component of the attributed NGHGH budget of the cut sites. The attributed GHG balance was positive for grazed sites (indicating a sink activity), but was negative for cut and mixed sites (indicating a source activity) (Table 2). Therefore, a grazing management seems to be a better strategy for removing GHG from the atmosphere than a cutting management. However, given that the studied sites differed in many respects (climate, soil and vegetation) (Soussana *et al.*, 2007), this hypothesis needs to be further tested.

Taken together, these results show that managed grasslands have a potential to remove GHG from the atmosphere, but that the utilisation of the cut herbage by ruminants may lead to large non-CO₂ GHG emissions in farm buildings, which may compensate this sink activity. Data from a larger number of flux sites and from long-term experiments will be required to upscale these results at regional scale and calculate GHG balance for a range of production systems. In order to further reduce uncertainties, C and N fluxes are investigated for a number of additional grassland and wetland sites (e.g. CarboEurope and NitroEurope research project). Grassland ecosystem simulation models have also been used for upscaling these fluxes (Levy *et al.*, 2007; Vuichard *et al.*, 2007a) in order to estimate the C and GHG balance at the scale of Europe. Two main problems were identified: (i) the lack of consistent grassland management data across Europe; (ii) the lack of detailed grassland soil C inventories for soil model initialisation (Vuichard *et al.*, 2007a).

Including carbon sequestration in greenhouse gas budgets at farm scale

A grazing livestock farm consists in a productive unit that converts various resources into outputs as milk, meat and sometimes grains too. In Europe, many ruminant farms have mixed farming systems: they produce themselves the roughage and, most often, part of the animal's feeds and even straw that is eventually needed for bedding. Conversely, these farms recycle animal manure by field application. Most farms purchase some inputs, such as fertilisers and feed, and they always use direct energy derived from fossil fuels. The net emissions of GHGs (methane, nitrous oxide and carbon dioxide) are related to C and nitrogen flows and to environmental conditions.

To date, only few recent models have been developed to estimate the farm GHG balance (Schils *et al.*, 2007). Most models have used fixed emission factors both for indoors and outdoors emissions (e.g. FARM GHG, Olesen *et al.*, 2006, Lovett *et al.*, 2006). Although, these models have considered the on- and off-farm CO₂ emissions (e.g. from fossil fuel combustion), they did not include possible changes in soil C resulting from the farm management. Moreover, as static factors are used rather than dynamic simulations, the environmental dependency of the GHG fluxes is not captured by these models.

A dynamic farm scale model (FarmSim) has been coupled to mechanistic simulation models of grasslands (PASIM, Riedo *et al.*, 1998; Vuichard *et al.*, 2007b) and croplands (CERES ECC). In this way, C sequestration by grasslands can be simulated (Soussana *et al.*, 2004) and included in the farm budget. The IPCC methodology Tier 1 and Tier 2 is used to calculate the CH₄ and N₂O emissions from cattle housing and waste management systems. The net GHG balance at the farm gate is calculated in CO₂ equivalents. Emissions induced by the production and transport of farm inputs (fuel, electricity, N fertilisers and feedstuffs) are calculated using a full accounting scheme based on life cycle analysis. The FarmSim model has been applied to seven contrasted cattle farms in Europe (Salètes *et al.*, 2004). The balance of the farm gate GHG fluxes leads to a sink activity for four out of the seven farms. When including pre-chain emissions related to inputs, all farms – but one – were found to be net sources of GHG. The total farm GHG balance varied between a sink of –70 and a source of +310 kg CO₂ equivalents per unit (GJ) energy in animal farm products. Byrne *et al.* (2007), measuring C balance for two dairy farms in South West Ireland, equally considered the farm perimeter as the system boundary for inputs and outputs of C. In the two case studies, both farms appeared as net C sinks, sequestering between 200 and 215 g C/m² per year (Table 1).

Farm scale mitigation options thus need to be carefully assessed at the production system scale, in order to minimise GHG emissions per unit meat or milk product (Schils *et al.*, 2007). Advanced (Tier 3) and verifiable methodologies still need to be developed in order to include GHG removals obtained by farm scale mitigation options in agriculture, forestry and land use (AFOLU sector, IPCC, 2006) national GHG inventories.

Conclusions

This review shows that grassland C sequestration is detected both by C stock change (inventories and long-term experiments) and by C flux measurements, however with high variability across studies. Further development of measurement methods and of plot and farm scale models carefully tested at benchmark sites will help further reduce uncertainties. Low cost mitigation options based on enhancing C sequestration in grasslands are available. Mitigating emissions and adapting livestock production systems to climate change will nevertheless require a major international collaborative effort and the development of extended observational networks combining C (and non-CO₂-GHG) flux measurements and long-term experiments to detect C stock changes. Carbon sequestration could play an important role in climate mitigation, but because of its potential reversibility preserving current soil C stocks and reducing CH₄ and N₂O emissions is strongly needed.

Acknowledgements

Tiphaine Tallec is funded by a research grant from the French Ministry for Research and Higher Education. This research

was funded by the EC FP6 'CarboEurope IP' and 'NitroEurope IP' projects.

References

- Allard V, Soussana JF, Falcimagne R, Berbigier P, Bonnefond JM, Ceschia E, D'hour P, Hénault C, Laville P, Martin C and Pinarès-Patino C 2007. The role of grazing management for the net biome productivity and greenhouse gas budget (CO₂, N₂O and CH₄) of semi-natural grassland. *Agriculture, Ecosystems and Environment* 121, 47–58.
- Ammann C, Flechard CR, Leifeld J, Neftel A and Fuhrer J 2007. The carbon budget of newly established temperate grassland depends on management intensity. *Agriculture Ecosystems and Environment* 121, 5–20.
- Baldocchi D and Meyers T 1998. On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agricultural and Forest Meteorology* 90, 1–25.
- Baldock JA and Skjemstad JO 2000. Role of the matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry* 31, 697–710.
- Balesdent J and Balabane M 1996. Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biology and Biochemistry* 28, 1261–1263.
- Bellamy PH, Loveland PJ, Bradley RI, Lark RM and Kirk GJD 2005. Carbon losses from all soils across England and Wales 1978–2003. *Nature* 437, 245–248.
- Beniston M 2004. The 2003 heat wave in Europe: a shape of things to come? An analysis based on Swiss climatological data and model simulations. *Geophysical Research Letters* 31, L02202, doi:10.1029/2003GL018857.
- Betts RA, Cox PM, Collins M, Harris PP, Huntingford C and Jones CD 2004. The role of ecosystem–atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. *Theoretical and Applied Climatology* 78, 157–175.
- Bird SB, Herrick JE, Wander MM and Wright SF 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. *Environmental Pollution* 116, 445–455.
- Boeckx P and Van Cleemput O 2001. Estimates of N₂O and CH₄ fluxes from agricultural lands in various regions in Europe. *Nutrient Cycling in Agroecosystems* 60, 35–47.
- Bony S, Colman R, Kattsov VM, Allan RP, Bretherton CS, Dufresne JL, Hall A, Hallegatte S, Holland MM, Ingram W, Randall DA, Soden DJ, Tselioudis G and Webb MJ 2006. How well do we understand and evaluate climate change feedback processes? *Journal of Climate* 19, 3445–3482.
- Bossuyt H, Six J and Hendrix PF 2005. Protection of soil carbon by microaggregates within earthworm casts. *Soil Biology and Biochemistry* 37, 251–258.
- Byrne KA, Kiely G and Leahy P 2005. CO₂ fluxes in adjacent new and permanent temperate grasslands. *Agricultural and Forest Meteorology* 135, 82–92.
- Byrne KA, Kiely G and Leahy P 2007. Carbon sequestration determined using farm scale carbon balance and eddy covariance. *Agriculture Ecosystems and Environment* 121, 357–364.
- Cannell MGR, Milne R, Hargreaves KJ, Brown TAW, Cruickshank MM, Bradley RI, Spencer T, Hope D, Billett MF, Adger WN and Subak S 1999. National inventories of terrestrial carbon sources and sinks: the UK experience. *Climatic Change* 42, 505–530.
- Chevallier T, Voltz M, Blanchart E, Chotte JL, Eschenbrenner V, Mahieu M and Albrecht A 2000. Spatial and temporal changes of soil C after establishment of a pasture on a long-term cultivated vertisol (Martinique). *Geoderma* 94, 43–58.
- Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T and Valentini R 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437, 529–533.
- Clayton H, McTaggart IP, Parker J, Swan L and Smith KA 1997. Nitrous oxide emissions from fertilised grassland: a 2-year study of the effects of N fertiliser form and environmental conditions. *Biology and Fertility of Soils* 25, 252–260.

- CLIMSOIL 2008. Review of existing information on the interrelations between soil and climate change. Final report of the ClimSoil project, contract number 070307/2007/486157/SE/B1. European Commission, December 2008.
- Conant RT, Paustian K and Elliott ET 2001. Grassland management and conversion into grassland: effects on soil carbon. *Ecological Applications* 11, 343–355.
- Conant RT, Easter M, Paustian K, Swan A and Williams S 2007. Impacts of periodic tillage on soil C stocks: a synthesis. *Soil and Tillage Research* 95, 1–10.
- Crutzen PJ, Mosier AR, Smith KA and Winiwarter W 2007. N₂O release from agro-biofuel production negates global warming reduction by replacing fossil fuels. *Atmospheric Chemistry and Physics Discussion* 7, 11191–11205.
- Davison B, Brunner A, Ammann C, Spirig C, Jocher M and Neftel A 2008. Cut-induced VOC emissions from agricultural grasslands. *Plant Biology* 10, 76–85.
- De Mazancourt C, Loreau M and Abbadie L 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* 79, 2242–2252.
- Delgado CL 2005. Rising demand for meat and milk in developing countries: implications for grasslands-based livestock production. In 'Grassland: a global resource', Proceedings of the XXth International Grassland Congress, Dublin, Ireland (ed. DA McGilloway), pp. 29–39. Wageningen Academic Publishers, Wageningen, The Netherlands.
- Dueck TA, de Visser R, Poorter H, Persijn S, Gorissen A, de Visser W, Shapendonk A, Vergahen J, Snel J, Harren FJM, Ngai AKY, Verstappen F, Bouwmeester H, Voeseek LACJ and Van Der Werf A 2007. No evidence for substantial aerobic methane emission by terrestrial plants: a ¹³C-labelling approach. *New Phytologist* 175, 29–35.
- Emmerich WE 2003. Carbon dioxide fluxes in a semiarid environment with high carbonate soils. *Agricultural and Forest Meteorology* 116, 91–102.
- Faverdin P, Maxin G, Chardon X, Brunschwig P and Vermorel M 2007. A model to predict the carbon balance of a dairy cow. In 'Elevage et environnement', Proceedings of the XIVth symposium Rencontres Recherches Ruminants, Paris, France, p. 66.
- Fearnside PM 2000. Global warming and tropical land-use change: Greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Climatic Change* 46, 115–158.
- Firbank LG, Smart SM, Crabb J, Crabb J, Critchley CNR, Fowbert JW, Fuller RJ, Gladders P, Green DB, Henderson I and Hill MO 2003. Agronomic and ecological costs and benefits of set-aside in England. *Agriculture Ecosystem and Environment* 95, 73–85.
- Fitter AH, Graves JD, Wolfenden J, Self GK, Brown TK, Bogie D and Mansfield TA 1997. Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. *New Phytologist* 137, 247–255.
- Flanagan LB, Weaver LA and Carlson PJ 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology* 8, 599–615.
- Flechar CR, Ambus P, Skiba U, Rees RM, Hensen A, van Amstel A, van den Pol-van Dasselaar A, Soussana JF, Jones M, Clifton-Brown J, Raschi A, Horvath L, Neftel A, Jocher M, Ammann C, Leifeld J, Fuhrer J, Calanca P, Thalman E, Pilegaard K, Di Marco C, Campbell C, Nemitz E, Hargreaves KJ, Levy PE, Ball BC, Jones SK, van de Bulk WCM, Groot T, Blom M, Domingues R, Kasper G, Allard V, Ceschia E, Cellier P, Laville P, Henault C, Bizouard F, Abdalla M, Williams M, Baronti S, Berretti F and Grosz B 2007. Effects of climate and management intensity on nitrous oxide emissions in grassland systems across Europe. *Agriculture Ecosystems and Environment* 121, 135–152.
- Flechar CR, Neftel A, Jocher M, Ammann C and Fuhrer J 2005. Bi-directional soil/atmosphere N₂O exchange over two mown grassland systems with contrasting management practices. *Global Change Biology* 11, 2114–2127.
- Follett RF, Samson-Liebig SE, Kimble JM, Pruessner E and Waltman SW 2001. Carbon sequestration under the conservation reserve program in the historic grazing land soils of the United States of America. In *Soil C sequestration and the greenhouse effect* (ed. R Lal), pp. 57, 27–40. Soil Science Society of America, Madison, WI.
- Follett RF, Kimble J, Leavitt SW and Pruessner E 2004. Potential use of soil C isotope analyses to evaluate paleoclimate. *Soil Science* 169, 471–488.
- Follett RF and Schuman GE 2005. Grazing land contributions to carbon sequestration. In 'Grassland: a global resource', Proceedings of the XXth International Grassland Congress, Dublin, Ireland (ed. DA McGilloway), pp. 265–277. Wageningen Academic Publishers, Wageningen, The Netherlands.
- Fontaine S, Mariotti A and Abbadie L 2003. The priming effect of organic matter: a question of microbial competition? *Soil Biology and Biochemistry* 35, 837–843.
- Fontaine S, Barot S, Barre P, Bdioui N, Mary B and Rumpel C 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450, 277–281.
- FAO 2006. Livestock's long shadows: environmental issues and options. FAO, Rome.
- Frank AB and Dugas WA 2001. Carbon dioxide fluxes over a northern, semiarid, mixed-grass prairie. *Agriculture and Forest Meteorology* 108, 317–326.
- Ganjugunte GK, Vance GF, Preston CM, Schuman GE, Ingram LJ, Stahl PD and Welker JM 2005. Soil organic carbon composition in a northern mixed-grass prairie: effects of grazing. *Soil Science Society of America Journal* 69, 1746–1756.
- Gilmanov T, Soussana JF, Aires L, Allard V, Amman C, Balzarolo M, Barcza Z, Bernhofer C, Campbell CL, Cernusca A, Cescatti A, Clifton-Brown J, Dirks BOM, Dore S, Eugster W, Fuhrer J, Gimeno C, Gruenwald T, Haszpra L, Hensen A, Ibrom A, Jacobs AFG, Jones MB, Lanigan G, Laurila T, Lohila A, Manca G, Marcolla B, Nagy Z, Pilegaard K, Pinter K, Raschi A, Rogiers N, Sanz MJ, Stefani P, Sutton M, Tuba Z, Valentini R, Williams ML and Wohlfahrt G 2007. Partitioning European grassland net ecosystem CO₂ exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agriculture, Ecosystems and Environment* 121, 93–120.
- Gilmanov TG, Tieszen LL, Wylie BK, Flanagan LB, Frank AB, Haferkamp MR, Meyers TP and Morgan JA 2005. Integration of CO₂ flux and remotely-sensed data for primary production and ecosystem respiration analyses in the Northern Great Plains: potential for quantitative spatial extrapolation. *Global Ecology and Biogeography* 14, 271–292.
- Goidts E and van Wesemael B 2007. Regional assessment of soil organic carbon changes under agriculture in Southern Belgium (1955–2005). *Geoderma* 141, 341–354.
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Joshi J, Jumpponen A, Korner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S and Lawton JH 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127.
- Hendriks DMD, van Huissteden J, Dolman AJ and van der Molen MK 2007. The full greenhouse gas balance of an abandoned peat meadow. *Biogeosciences* 4, 411–424.
- Hunt JE, Kelliher FM, McSeveny TM, Ross DJ and Whitehead D 2004. Long-term carbon exchange in a sparse, seasonally dry tussock grassland. *Global Change Biology* 10, 1785–1800.
- IPCC 1996. Revised guidelines for national greenhouse gas inventories. IPCC, Cambridge University Press, Cambridge.
- IPCC 2001. Climate change 2001: the scientific basis (Contribution of Working Group I to the third assessment report of the IPCC). Cambridge University Press, Cambridge.
- IPCC 2006. Good practice guidance on land use change and forestry in national greenhouse gas inventories. IPCC, Institute for Global Environmental Strategies, Tokyo, Japan.
- IPCC 2007. Climate change 2007: the scientific basis (Contribution of Working Group I to the third assessment report of the IPCC). Cambridge University Press, Cambridge.
- Jaksic V, Kiely G, Albertson J, Oren R, Katul G, Leahy P and Byrne KA 2006. Net ecosystem exchange of grassland in contrasting wet and dry years. *Agricultural and Forest Meteorology* 139, 323–334.
- Janssens IA, Freibauer A, Ciais P, Smith P, Nabuurs GJ, Folberth G, Schlamadinger B, Hutjes RWA, Ceulemans R, Schulze ED, Valentini R and Dolman AJ 2003. Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO₂ emissions. *Science* 300, 1538–1542.
- Jones MB and Donnelly A 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO₂. *New Phytologist* 164, 423–439.
- Keppler F, Hamilton JTG, Brass M and Rockmann T 2006. Methane emissions from terrestrial plants under aerobic conditions. *Nature* 439, 187–191.
- Klein JA, Harte J and Zhao XQ 2005. Dynamic and complex microclimate responses to warming and grazing manipulations. *Global Change Biology* 11, 1440–1451.

- Klumpp K, Soussana JF and Falcimagne R 2007. Effects of past and current disturbance on carbon cycling in grassland mesocosms. *Agriculture Ecosystems and Environment* 121, 59–73.
- Klumpp K and Soussana JF 2009. Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect approach. *Global Change Biology*, doi:10.1111/j.1365-2486.2009.01905.x (in press; available on line).
- Lal R 1999. Long-term tillage and wheel traffic effects on soil quality for two central Ohio soils. *Journal of Sustainable Agriculture* 14, 67–84.
- Lal R 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* 304, 1623–1627.
- Leahy P, Kiely G and Scanlon TM 2004. Managed grasslands: a greenhouse gas sink or source? *Geophysical Research Letters* 31, L20507, doi:10.1029/2004GL021161.
- Lehner B, Doll P, Alcamo J, Henrichs T and Kaspar F 2006. Estimating the impact of global change on flood and drought risks in Europe: a continental, integrated analysis. *Climatic Change* 75, 273–299.
- Lemaire G and Chapman D 1996. Tissue flows in grazed plant communities. In *The ecology and management of grazing systems* (ed. J Hodgson and AW Illius), pp. 3–35. CAB International, Wallingford, UK.
- Letten S, Van Orshoven J, van Wesemael B, De Vos B and Muys B 2005b. Stocks and fluxes of soil organic carbon for landscape units in Belgium derived from heterogeneous data sets for 1990 and 2000. *Geoderma* 127, 11–23.
- Letten S, van Orshoven J, van Wesemael B, Muys B and Perrin D 2005a. Soil organic carbon changes in landscape units of Belgium between 1960 and 2000 with reference to 1990. *Global Change Biology* 11, 2128–2140.
- Levy PE, Mobbs DC, Jones SK, Milne R, Campbell C and Sutton MA 2007. Simulation of fluxes of greenhouse gases from European grasslands using the DNDC model. *Agriculture, Ecosystems and Environment* 121, 186–192.
- Lloyd CR 2006. Annual carbon balance of a managed wetland meadow in the Somerset Levels, UK. *Agricultural and Forest Meteorology* 138, 168–179.
- Loiseau P and Soussana JF 1999. Elevated CO₂, temperature increase and N supply effects on the accumulation of below-ground carbon in a temperate grassland ecosystem. *Plant and Soil* 212, 123–134.
- Lovett DK, Shalloo L, Dillon P and O'Mara FP 2006. A systems approach to quantify greenhouse gas fluxes from pastoral dairy production as affected by management regime. *Agricultural Systems* 88, 156–179.
- Martin C, Morgavi DP and Doreau M 2009. Methane mitigation in ruminants: from microbe to the farm scale. *Animal* (in press).
- Meehl GA and Tebaldi C 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305, 994–997.
- Morgan JA, Pataki DE, Korner C, Clark H, Del Grosso SJ, Grunzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, Nippert JB, Nowak RS, Parton WJ, Polley HW and Shaw MR 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia* 140, 11–25.
- Nelson JD, Schoenau JJ and Malhi SS 2008. Soil organic carbon changes and distribution in cultivated and restored grassland soils in Saskatchewan. *Nutrient Cycling in Agroecosystem* 82, 137–148.
- Nieveen JP, Campbell DI, Schipper LA and Blair IANJ 2005. Carbon exchange of grazed pasture on a drained peat soil. *Global Change Biology* 11, 607–618.
- Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myrneni RB and Running SW 2003. Climate-driven increases in global terrestrial net Primary production from 1982 to 1999. *Science* 300, 1560–1563.
- Ogle SM, Conant RT and Paustian K 2004. Deriving grassland management factors for a carbon accounting method developed by the Intergovernmental Panel on Climate Change. *Environmental Management* 33, 474–484.
- Ojima DS, Parton WJ, Schimel DS, Scurlock JMO and Kittel TGF 1993. Modeling the effects of climatic and CO₂ changes on grassland storage of soil C. *Water, Air, and Soil Pollution* 70, 643–657.
- Olesen JE, Schelde K, Weiske A, Weisbjerg MR, Asman WAH and Djurhuus J 2006. Modelling greenhouse gas emissions from European conventional and organic dairy farms. *Agriculture Ecosystems and Environment* 112, 207–220.
- Paustian K, Cole CV, Sauerbeck D and Sampson N 1998. CO₂ mitigation by agriculture: an overview. *Climatic Change* 40, 135–162.
- Personeni E and Loiseau P 2004. How does the nature of living and dead roots affect the residence time of carbon in the root litter continuum? *Plant and Soil* 267, 129–141.
- Personeni E and Loiseau P 2005. Species strategy and N fluxes in grassland soil – a question of root litter quality or rhizosphere activity? *European Journal of Agronomy* 22, 217–229.
- Petersen BM, Olesen JE and Heidmann T 2002. A flexible tool for simulation of soil carbon turnover. *Ecological Modelling* 151, 1–14.
- Phillips RL and Beeri O 2008. Scaling-up knowledge of growing-season net ecosystem exchange for long-term assessment of North Dakota grasslands under the Conservation Reserve Program. *Global Change Biology* 14, 1008–1017.
- Piao S, Fang J, Ciais P, Peylin P, Huang Y, Sitch S and Wang T 2009. The carbon balance of terrestrial ecosystems in China. *Nature* 458, 1009–1013.
- Picon-Cochard P, Teyssonneyre F, Besle JM and Soussana JF 2004. Effects of elevated CO₂ and cutting frequency on the productivity and herbage quality of a semi-natural grassland. *European Journal of Agronomy* 20, 363–377.
- Pinares-Patino CS, D'Hour P, Jouany JP and Martin C 2007. Effects of stocking rate on methane and carbon dioxide emissions from grazing cattle. *Agriculture Ecosystems and Environment* 121, 30–46.
- Potter KN, Torbert HA, Johnson HB and Tischler CR 1999. Carbon storage after long-term grass establishment on degraded soils. *Soil Science* 164, 718–725.
- Rémy JC and Marin-La Flèche A 1976. L'entretien organique des terres. Coût d'une politique de l'humus. *Entreprises Agricoles* 11, 63–67.
- Reynolds SG, Batello C, Baas S and Mack S 2005. Grassland and forage to improve livelihoods and reduce poverty. In 'Grassland: a global resource', Proceedings of the XXth International Grassland Congress, Dublin, Ireland (ed. DA McGilloway), pp. 323–338. Wageningen Academic Publishers, Wageningen, The Netherlands.
- Riedo M, Grub A, Rosset M and Fuhrer J 1998. A pasture simulation model for dry matter production and fluxes of carbon, nitrogen, water and energy. *Ecological Modelling* 105, 141–183.
- Robertson GP, Paul EA and Harwood RR 2000. Greenhouse gases in intensive agriculture: contributions of individual gases to the radiative forcing of the atmosphere. *Science* 289, 1922–1925.
- Robles MD and Burke IC 1998. Soil organic matter recovery on conservation reserve program fields in southeastern Wyoming. *Soil Science Society of America Journal* 62, 725–730.
- Rogiers N, Conen F, Furger M, Stöckli R and Eugster W 2008. Impact of past and present land-management on the C-balance of a grassland in the Swiss Alps. *Global Change Biology* 14, 2613–2625.
- Röscher C, Temperton VM, Scherer-Lorenzen M, Schmitz M, Schumacher J, Schmid B, Buchmann N, Weisser WW and Schulze ED 2005. Overyielding in experimental grassland communities – irrespective of species pool or spatial scale. *Ecology Letters* 8, 419–429.
- Salètes S, Fiorelli JL, Vuichard N, Cambou J, Olesen JE, Hacala S, Sutton M, Fuhrer J and Soussana JF 2004. Greenhouse gas balance of cattle breeding farms and assessment of mitigation option. In *Greenhouse Gas Emissions from Agriculture Conference*, Leipzig, Germany (10–12 February 2004), pp. 203–208.
- Schär C and Jendritzky G 2004. Climate change: hot news from summer 2003. *Nature* 432, 559–560.
- Schils RLM, Olesen JE, del Prado A and Soussana JF 2007. A review of a farm level modelling approach for mitigating greenhouse gas emissions from ruminant livestock systems. *Livestock Science* 112, 240–251.
- Schlesinger WH 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* 348, 232–234.
- Siemens J 2003. The European carbon budget: a gap. *Science* 302, 1681–1681.
- Six J, Callewaert P, Lenders S, De Gryze S, Morris SJ, Gregorich EG, Paul EA and Paustian K 2002. Measuring and understanding carbon storage in afforested soils by physical fractionation. *Soil Science Society of America Journal* 66, 1981–1987.
- Skiba U and Smith KA 2000. The control of nitrous oxide emissions from agricultural and natural soils. *Chemosphere Global Change Science* 2, 379–386.
- Smith JU, Smith P, Wattenbach M, Zaehle S, Hiederer R, Jones RJA, Montanarella L, Rounsevell M, Reginster I and Ewert F 2005. Projected changes in mineral soil carbon of European croplands and grasslands, 1990–2080. *Global Change Biology* 11, 2141–2152.
- Smith P, Chapman SJ, Scott WA, Black HJ, Wattenbach M, Milne R, Campbell CD, Lilly A, Ostle N, Levy PE, Lumsdon DG, Millard P, Towers W, Zaehle Z and Smith JU 2007. Climate change cannot be entirely responsible for soil carbon loss observed in England and Wales, 1978–2003. *Global Change Biology* 13, 2605–2609.

- Sommer SG, Petersen SO and Moller HB 2004. Algorithms for calculating methane and nitrous oxide emissions from manure management. *Nutrient Cycling in Agroecosystems* 69, 143–154.
- Soussana JF and Hartwig UA 1996. The effects of elevated CO₂ on symbiotic N₂ fixation: a link between the carbon and nitrogen cycles in grassland ecosystems. *Plant and Soil* 187, 321–332.
- Soussana JF, Casella E and Loiseau P 1996. Long-term effects of CO₂ enrichment and temperature increase on a temperate grass sward. 2. Plant nitrogen budgets and root fraction. *Plant and Soil* 182, 101–114.
- Soussana JF, Allard V, Pilegaard K, Ambus C, Campbell C, Ceschia E, Clifton-Brown J, Czobel S, Domingues R, Flechard C, Fuhrer J, Hensen A, Horvath L, Jones M, Kasper G, Martin C, Nagy Z, Neftel A, Raschi A, Baronti S, Rees RM, Skiba U, Stefani P, Manca G, Sutton M, Tuba Z and Valentini R 2007. Full accounting of the greenhouse gas (CO₂, N₂O, CH₄) budget of nine European grassland sites. *Agriculture, Ecosystems and Environment* 121, 121–134.
- Soussana JF, Loiseau P, Vuichard N, Ceschia E, Balesdent J, Chevallier T and Arrouays D 2004. Carbon cycling and sequestration opportunities in temperate grasslands. *Soil Use and Management* 20, 219–230.
- Suyker AE and Verma SB 2001. Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biology* 7, 279–289.
- Teyssonneyre F, Picon-Cochard C, Falcimagne R and Soussana JF 2002. Effects of elevated CO₂ and cutting frequency on plant community structure in a temperate grassland. *Global Change Biology* 8, 1034–1046.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, De Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, Van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL and Williams SE 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thomsen IK and Olesen JE 2000. C and N mineralization of composted and anaerobically stored ruminant manure in differently textured soils. *Journal of Agricultural Sciences, Cambridge* 135, 151–159.
- Thuiller W, Lavorel S, Araujo MB, Sykes MT and Prentice IC 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102, 8245–8250.
- Tilman D, Lehman CL and Thomson KT 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America* 94, 1857–1861.
- Tilman D, Reich PB and Knops JMH 2006a. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441, 629–632.
- Tilman D, Reich PB and Knops JMH 2006b. Carbon-negative biofuels from low-input high diversity grassland biomass. *Science* 314, 1598–1600.
- Tubiello F, Soussana JF, Howden SM and Easterling W 2007. Crop and pasture response to climate change. *Proceedings of the National Academy of Sciences of the United States of America* 104, 19686–19690.
- US-EPA 2006. Global anthropogenic non-CO₂ greenhouse gas emissions: 1990–2020 (EPA 430-R-06-003), US-EPA, Washington, DC.
- Van der Werf GR, Randerson JT, Giglio L, Collatz GJ, Kasibhatla PS and Arellano AF 2006. Interannual variability in global biomass burning emissions from 1997 to 2004. *Atmospheric Chemistry and Physics* 6, 3423–3441.
- Van Oost K, Quine TA, Govers G, De Gryze S, Six J, Harden JW, Ritchie JC, McCarty GW, Heckrath G, Kosmas C, Giraldez JV, da Silva JRM and Merckx R 2007. The impact of agricultural soil erosion on the global carbon cycle. *Science* 318, 626–629.
- Velthof GL and Oenema O 1997. Nitrous oxide emission from dairy farming systems in the Netherlands. *Netherlands Journal of Agricultural Science* 45, 347–360.
- Vleeshouwers LM and Verhagen A 2002. Carbon emission and sequestration by agricultural land use: a model study for Europe. *Global Change Biology* 8, 519–530.
- Vuichard N, Ciais P, Viovy N, Calanca P and Soussana JF 2007a. Estimating the greenhouse gas fluxes of European grasslands with a process-based model: 2. Simulations at the continental level. *Global Biogeochemical Cycles* 21, GB1005, doi:10.1029/2005GB002612.
- Vuichard N, Soussana JF, Ciais P, Viovy N, Ammann C, Calanca P, Clifton-Brown J, Fuhrer J, Jones M and Martin C 2007b. Estimating the greenhouse gas fluxes of European grasslands with a process-based model: 1. Model evaluation from *in situ* measurements. *Global Biogeochemical Cycles* 21, GB1004, doi:10.1029/2005GB002611.
- Xu LK and Baldocchi DD 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agricultural and Forest Meteorology* 123, 79–96.
- Zavaleta ES, Shaw MR, Chiariello NR, Mooney HA and Field CB 2003. Additive effects of simulated climate changes, elevated CO₂, and nitrogen deposition on grassland diversity. *Proceedings of the National Academy of Sciences of the United States of America* 100, 7650–7654.